305 -1976

5 -1976 /

epartment of Agriculture
nd Fisheries for Scotland

LIBRARY
SEP 16 1976
FISH & WILDLIFE SERVICE

Simulation of Vertical Structure in a Planktonic Ecosystem

J H Steele and
E W Henderson

Scottish Fisheries Research
Report number 5 1976

P

CONTENTS

Introduction Page 1

General Description 1

Boundary conditions at surface and bottom 5

Forward difference 5

Du Fort-Frankel 5

Photosynthesis 6

Sinking of phytoplankton 6

Phytoplankton production (PR) 7

Zooplankton grazing 7

Zooplankton metabolism 7

Zooplankton growth 8

Zooplankton reproduction 8

Zooplankton mortality 9

Variables and Coefficients 9

Subscripted variables 9

Coefficients 10

Numerical values used for basic run 11

Coefficients 12

Presentation 14

Test Runs 16

Flow Diagram 16

Statement Lists 19

Summary 21

References 21

Appendix I : Initial Parameters 22

Appendix II : Program listing 23

Scottish Fisheries Research Report Number 5 1976

Simulation of Vertical Structure in a Planktonic Ecosystem

J H Steele and E W Henderson

Marine Laboratory Aberdeen

Introduction

The study of planktonic ecosystems requires understanding of the interactions between phytoplankton and zooplankton. Plant growth, however, depends on the concentration in the water of essential nutrients, such as nitrate, and these depend in turn on processes of vertical exchange. Further changes in the zooplankton population need to be considered in terms of the growth cycle of copepods from eggs to adults, and of predation at various stages in the life cycle. The last aspect is particularly relevant to problems concerning availability of food to fish larvae where it is not the total zooplankton biomass that is important but the numbers of those sizes of copepod which are suitable as food. For these reasons the interactions to be explored must begin with vertical mixing processes in the water column and produce, as output, the weight and numbers of copepods in different cohorts.

Any complete description of the planktonic ecosystem requires consideration of horizontal as well as vertical variation in nutrients, phytoplankton and zooplankton. It might be possible, numerically, to construct such a model with considerable detail in these dimensions as well as of biological structure. Conceptually, however, it is better to investigate these dimensions separately before combining them in a much larger model. Further, experimental work in long plastic columns (Davies, Gamble and Steele, 1975) provides data on changes in the vertical dimension only and the model developed here is intended to provide a basis for interpretation of these data.

General Description

The aim of the simulation is to describe changes with time in a vertical column of water. The driving mechanisms are provided by vertical turbulence and light energy. The main state variables are nutrients, phytoplankton and herbivores. The model is applicable to a laterally homogeneous sea or to an enclosure which isolates a column of water.

The driving mechanisms can either be applied at a fixed rate, such that incident radiation, attenuation and vertical diffusivity are constant with time, or they can be given day-to-day variation. These could be handled in a sub-model which gives, as functions of depth, the diffusivity (DIF) and the photosynthetic rate (PH) without nutrient limitation. Thus the input parameters in the main model are *DIF* and *PH*.

The nutrients are represented by a single parameter R, variable with depth, which is taken to be the concentration of soluble nitrogen compounds available to the phytoplankton. It is assumed that all components of the ecosystem have a fixed C/N ratio; R can therefore be expressed in "carbon" units, so that one unit of measurement can be used for the whole model. It would be equally possible to use nitrogen as the common unit. The uptake of R by the phytoplankton is assumed to follow a hyperbolic curve. Because of the use of a fixed C/N ratio, uptake then becomes proportional to growth.

The phytoplankton are represented by one parameter, *P*, expressed in units of carbon. The growth rate varies with *PH* and nutrient concentration *R*, which are themselves depth dependent. A sinking term is introduced which is also dependent on *R* (Steele and Yentsch, 1960). At present no attempt is made to include the carbon/chlorophyll ratio.

The herbivores, assumed to belong to one species of copepod, are defined by two basic parameters: *W*, the weight of an individual copepod with limits of *WO*, the initial weight, and *W2*, the weight of the adult; *Z*, the number of individuals of weight *W*. To represent a population with copepods of different ages, six cohorts are used so that we have W(J), Z(J), where J = 1, 6. When any cohort reaches the adult stage it is assumed to spend a fixed period in this stage during which food intake is used for reproduction and at the end of which a new cohort is started. The herbivores are assumed to graze over the whole of the vertical water column, either equally at all depths, or in proportion to the phytoplankton available. Thus the herbivore concentrations are not directly a function of the depth z.

The herbivores excrete nutrients in solution and these are presumed to be returned to the water column immediately after ingestion. They also excrete nutrients as faecal material and this is taken to be completely lost to the bottom (Steele and Baird, 1972) until it is returned from there as this material is utilised by the benthos. The growth of the copepods is balanced by predation on them (as a functional relation rather than a real predator) but, again, it is assumed that the nutrient content removed in this way is lost from the system. Since the system would run down as a result of nutrient loss, this is balanced by an input from the bottom.

Normally the model can be run for a simulation of 300 days. Such a long period is used to give some idea of the stability of the whole system when constant *DIF* and *PH* are used. The print-out of data gives the average concentration of *R* and *P* in twelve vertical layers at daily intervals. The individual weights W(J) and numbers Z(J) of the six cohorts are also given at daily intervals. As a summary of these data, the average *R* and *P* for the whole water column are given, together with the total herbivore biomass (the sum of W(J). Z(J)). All these variables can be presented graphically by a plotter program.

Derivation of the Equations

The main problems of simulation lie in the equations for nutrient concentrations *R* and phytoplankton *P*. These equations are

$$\frac{\partial R}{\partial t} = EX - PR + \frac{\partial}{\partial z} \lambda_z \frac{\partial R}{\partial z} \qquad - (1)$$

$$\frac{\partial P}{\partial t} = PR - GR - V_z \frac{\partial P}{\partial z} + \frac{\partial}{\partial z} \lambda_z \frac{\partial P}{\partial z} \qquad - (2)$$

EX (excretion), PR (production), GR (grazing) are complicated functions of *P, R, W, Z* and provide the links between (1), (2) and the equations for *Z* and *W* which will be treated later. $V_z = V_z(R)$ is the sinking rate of *P*. λ_z is the vertical eddy diffusivity.

Equations (1) and (2) could be converted directly into finite difference form. Instead they are converted into an integral form and then averaged. There are several reasons for doing this. Firstly, the equations for *Z* and *W* depend on the average quantity of *P* in each layer of the water column and this is obtain- obtained more easily from the integrated form. More important are problems associated with the boundary conditions. If the air-sea boundary is put at $z = 0$ and the sea-bottom at $z = H$, then, in reality, $\lambda_z \to 0$ as $z \to 0, H$.

This happens in thin boundary layers, whereas the vertical steps used here are relatively thick, 1-2m. Also the use of a sinking term in P with no input through the surface would mean, theoretically, that $P = 0$ at $z = 0$. Since, in practice, we cannot sample this near surface microstructure and it would be too difficult to simulate it numerically, it is easier to consider average conditions in thicker layers, especially at surface and bottom.

Consider equation (2) for a layer of thickness, h

$$\frac{\partial}{\partial t}\int_z^{z+h} P\,dz = \int_z^{z+h} (PR-GR)\;dz - \int_z^{z+h} V_z \frac{\partial P}{\partial z}\,dz + \left[\lambda_z \frac{\partial P}{\partial z}\right]_z^{z+h}$$

Taking averages over the layer and letting $P_z = \frac{1}{h}\int_z^{z+h} P\,dz$

$$\frac{\partial P_z}{\partial t} = \overline{PR} - \overline{GR} + \frac{1}{h}(V_{z-h}\,P_{z-h} - V_z\,P_z) + \frac{1}{h}2\left[\lambda_{z+h}\,(P_{z+h} - P_z) - \lambda_z\,(P_z - P_{z-h}\right.$$

For a single forward difference with k as the time step, in the usual notation (dropping the averages on PR & GR) with m and n representing space and time respectively)

$$P_m^{n+1} - P_m^n = (PR_m^n - GR_m^n)\,k + (V_{m-1}^n\,P_{m-1}^n - V_m^n\,P_m^n)\,k/h$$

$$+ \left[\lambda_{m+1}\,(P_{m+1}^n - P_m^n) - \lambda_m\,(P_m^n - P_{m-1}^n)\right] k/h^2 \qquad - (3)$$

with the stability condition that $\lambda\ k/h^2 < 1/2$ (where $\lambda = \max.\ \lambda_m$)

For a three level explicit scheme

$$P_m^{n+1} - P_m^{n-1} = (PR_m^n - GR_m^n)\,2k + (V_{m-1}^n\,P_{m-1}^n - V_m^n\,P_m^n)\,2\,k/h$$

$$+ \left[\lambda_{m+1}\,P_{m+1}^n + \lambda_m\,P_{m-1}^n - P_m^n\,(\lambda_{m+1} + \lambda_m)\right] 2k/h^2$$

To convert this into a Du Fort-Frankel (1953) scheme, for stability, it is essential that the "leap-frog" be used for *all* terms. Thus we use only the 'o' terms in Fig. 1a.

$$\overline{PR}_m = \tfrac{1}{2}\,(PR_{m-1}^n + PR_{m+1}^n)$$

$$\overline{GR}_m = \tfrac{1}{2}\,(GR_{m-1}^n + GR_{m+1}^n)$$

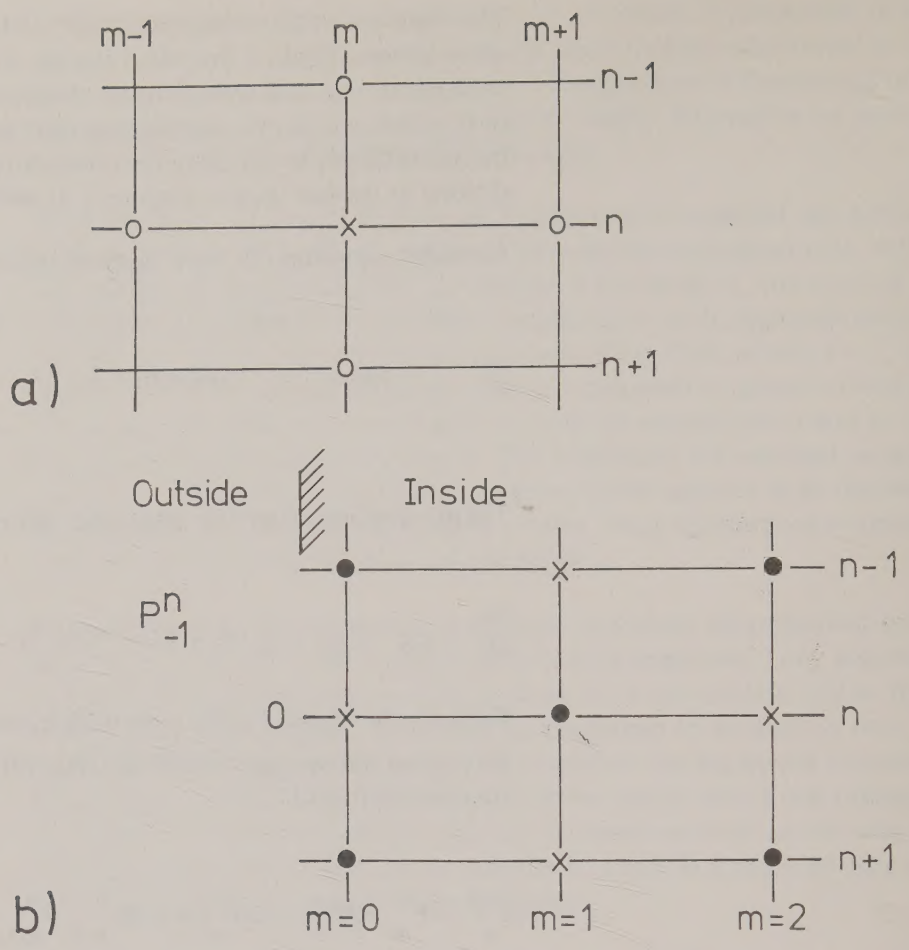

Figure 1 a. Space (m) and time (n) grid for numerical analysis.
1 b. Boundary grid.

In the sinking term $V^n_m\ P^n_m$ is replaced by $\frac{1}{2}(V^n_{m+1}\ P^n_{m+1} + V^n_{m-1}\ P^n_{m-1})$ and in the diffusion term P^n_m is replaced by $(P^{n+1}_m + P^{n-1}_m)/2$ to give

$$P^{n+1}_m - P^{n-1}_m = (\overline{PR}_m - \overline{GR}_m)\ 2k + (V^n_{m-1}\ P^n_{m-1} - V^n_{m+1}\ P^n_{m+1})\ k/h$$
$$+ \boxed{\lambda_{m+1}\ P^n_{m+1} + \lambda_m\ P^n_{m-1} - \tfrac{1}{2}(\lambda_{m+1} + \lambda_m)(P^{n+1}_m - P^{n-1}_m)}\ 2k/h^2$$

$$P^{n+1}_m\ (1 + (\lambda_{m+1} + \lambda_m)\ k/h^2) = \boxed{(PR^n_{m+1} + PR^n_{m-1}) - (GR^n_{m+1} + GR^n_{m-1})}$$
$$+ \boxed{(V^n_{m-1}\ P^n_{m-1} - V^n_{m+1}\ P^n_{m+1})/h}\ k + (\lambda_{m+1}\ P^n_{m+1} + \lambda_m\ P^n_{m-1})\ 2k/h^2$$
$$+ P^{n-1}_m\ (1 - (\lambda_{m+1} + \lambda_m)\ k/h^2) \qquad -(4)$$

Similar equations can be derived for R_i for forward difference (FD)

$$R^{n+1}_m - R^n_m = (EX^n_m - PR^n_m)\ k + \boxed{\lambda_{m+1}(R^n_{m+1} - R^n_m) - \lambda_m(R^n_m - R^n_{m-1})}\ k/h^2$$
$$-(5)$$

for Du Fort-Frankel (DFF)

$$R^{n+1}_m\ (1 + (\lambda_{m+1} + \lambda_m)\ k/h^2) = \boxed{(EX^n_{m+1} + EX^n_{m-1}) - PR^n_{m+1} + PR^n_{m-1}}\ k$$
$$+ (\lambda_{m+1}\ R^n_{m+1} + \lambda_m\ R^n_{m-1})\ 2k/h^2 + R^{n-1}_m\ \boxed{1 - (\lambda_{m+1} + \lambda_m)\ k/h^2}$$
$$-(6)$$

DFF is used as the main technique because there are no strict limits on the time step. However, for starting up, FD must be used. To provide a check on both methods the program is written so that the FD can be used for a variable number of steps. Thus a comparison can be made between FD over the entire run and DFF for all except the first time step. (Detailed differences arise because of depth averaging procedures in DFF but there is no long-term divergence in the general character of the results).

Boundary conditions at surface and bottom

Forward difference

At $m = 0$, i.e. in the layer $(0, h)$, the flux of P out of this layer is

$$V_o^n P_o^n /h - \lambda_1 (P_1^n - P_o^n) / h^2$$

since there is no sinking or mixing across the upper boundary. By comparison with (3) this can be obtained by taking $V_{-1}^n = \lambda_o = 0$
(P_{-1}^n can take any value but it is easiest to put $P_{-1}^n = 0$).
The same conditions (including $R_{-1}^n = 0$) satisfy the upper boundary requirements for R.

At $z = H$ there is no mixing but material sinks out. Taking $m = M$ for the layer $(H - h, H)$, the flux of P is $(V_M^n P_M^n - V_{M-1}^n P_{M-1}^n) /h + \lambda_M (P_M^n - P_{M-1}^n) /h^2$
This is obtained by taking $\lambda_{M+1} = 0$ (P_{M+1}^n can take any value).

The flux of R at $z = H$ involves a return of nutrient to the water from the bottom. This is taken to occur at a fixed daily rate of increase of concentration, ADDR, in the bottom layer. This would require an extra term in equation (5) for this layer

$$R_M^{n+1} = R_M^n + k.ADDR + \text{remaining terms}$$

In the program this is carried out later as a separate step.
(In Fortran notation R(M) = R(M)+k*ADDR).

Du Fort-Frankel

For the diffusion terms the same boundary conditions hold

$$\lambda_o = \lambda_{M+1} = 0$$

For the other terms it is not permissible to use the central values P_m^n, R_m^n directly. A "predictor-corrector" type of procedure is used after the interior values have been found. A value for P_o^n based on "approved" grid points (Fig. 1b) would be $P_o^n = P_o^{n-1} + \frac{1}{2} (P_2^{n+1} - P_2^{n-1})$

$$\therefore P_{-1}^n = 2P_o^n - P_1^n = 2P_o^{n-1} + P_2^{n+1}$$

$$- P_2^{n-1} - P_1^n$$

Similarly for R^n_{-1}, R^n_{M+1}, P^n_{M+1}

At $m = 0$ $V^n_{-1} = 0$ and P^n_{-1} can take any value

For layer $m = M$, V_{M+1} is defined using R_{M+1} (V is a function of R).

$\overline{PR}$, $\overline{GR}$ and $\overline{EX}$ are calculated using these values.

For the nutrient addition in the bottom layer

$R^{n+1}_M = 2k.ADDR/(1 + \lambda_M k/h^2)$ + other terms

This is added in the R(M) as a separate step.

Photosynthesis

As a description of the relation between photosynthetic rate, *PH*, and light-intensity, *I*,

$$PH = \frac{A\,I}{I_o} \exp(-2I/I_o) \qquad \text{(Steele, 1962)}$$

where $I = I_o\, e^{-Kz}$ and K is the extinction coefficient.

The form of this relation assumes that PH has a maximum value at $I = 0.5\, I_o$ and this value is 0.184 A. Thus A can be defined by assuming a value for PH max.

$$\int_z^{z+h} PH\,dz = \int_{I_z}^{I_{z+h}} -\frac{A}{KI_o} \exp(-2I/I_o)\,dI$$

$$= \frac{A}{2K}\left[\exp(-2I_{z+h}/I_o) - \exp(-2I_z/I_o)\right]$$

Thus $PH_m = \frac{A}{2Kh}\left[\exp(-2e^{-Kz_m}) - \exp(-2e^{-K(z_m+h)})\right]$

This relation can be used either to provide a fixed PH over a whole simulation or a PH varying on a day-to-day basis as a function of I_o and k.

Sinking of phytoplankton

The sinking rate of phytoplankton is a function of the size of cell, temperature, nutrient "condition" and probably many other factors. Only the effect of nutrients is introduced here following Steele & Yentsch (1960). This assumes that when a cell is deprived of nutrient it sinks faster than it does with no deprivation. The problem is to define this deprivation. Experiments and field data suggest that response to external nutrient concentration is sufficiently rapid that, as a first approximation, the effect can be expressed in terms of R_m. Even given this, the functional form of the relation is not known. It will be assumed here that

$$V_m = V\,(1 - R_m/R_{max}) \qquad R_m < R_m$$

$$= 0 \qquad R_m \gg R_{max}$$

where V is a constant for the system.

Phytoplankton production (PR)

This term links the input function PH with the other processes. PH_m is assumed to be an estimate of the average photosynthetic rate per unit of plant carbon in layer m when nutrients are not limiting. Essentially, PH_m is a function of light energy available at that depth.
Nutrient limitation has the form

$$R_m^n / (A + R_m^n)$$

where A is the "half-saturation" parameter and the maximum rate (V_{max}) comes from PH_m. The respiration rate RE is assumed to be dependent only on plant carbon concentration. Thus

$$PR_m^n = (PH_m \, R_m^n / (A + R_m^n) - RE) \, P_m^n$$

The values for PH_m are taken to be daily averages so that, even when time intervals shorter than one day are used, the PH value has no component for diurnal variation.

Zooplankton grazing

It is assumed that grazing rate is a function of the weight of the individual copepod and this relation is taken as $W^{0.7}$. If W_j is the weight of the animals in cohort j, and z_j is the number in that cohort, then for six cohorts total grazing will be proportional to

$$\sum_{j=1}^{6} z_j \, W_j^{0.7} \qquad - (7)$$

This will apply to the whole water column but grazing in each layer will depend on the time spent by the population in that layer. There are two strategies used here: (1) equal time at all layers, (2) time in any layer proportional to the food supply, P_m, in that layer. By using a coefficient B, $0 \leqslant B \leqslant 1$, varying proportions of the two behaviours can be introduced by the term

$$B/M + (1-B)P_m / \sum_M P_M \qquad - (8)$$

Grazing rate is also dependent on plant concentration and a hyperbolic type of relation is used

$$C \; (P_m - PO)/D + P_m - PO) \; P_m \rangle \; PO \qquad - (9)$$

This gives a threshold PO below which grazing is taken to be zero.
C and D are constants.

Thus combining (7), (8) and (9) gives an expression for GR_m

$$GR_m = \frac{1}{h} \bullet (\sum_j Z_j W_j^{0.7})(B/M + (1-B)P_m / \sum_M P_m) \, C \, (P_m - PO)/D + P_m - PO)$$

Zooplankton metabolism

Food assimilated is a fraction of that ingested. It is assumed that this fraction is constant with a value of 0.7. The un-assimilated food is assumed to be excreted as faecal pellets which sink rapidly and are lost to the system. Of the food assimilated, some goes to growth and reproduction and the remainder supplies respiration needs. It is assumed that the nitrogen equivalent of the carbon metabolized is released immediately in a form accessible to phytoplankton. No difference is considered between the forms of available nitrogen.

It is assumed that the metabolic rate has two components; a basal rate, F dependent only on weight as $W^{0.7}$; and a component, E, proportional to the food assimilated (specific dynamic action).

Zooplankton growth

Total food intake by all copepods = $h \bullet \sum_{M} GR_m$

Intake by one copepod = $W_j^{0.7} h \, \Sigma GR_m / \Sigma Z_j W_j^{0.7}$

Of this, 0.7 will be assimilated and of the assimilated food E will be used for associated metabolism. At the same time there is a basal metabolic loss of $F. W^{0.7}$. In total, then

$$\frac{dWj}{dt} = \left[h \, 0.7(1-E) \, \Sigma \, GR_m / \Sigma \, Z_j \, W_j^{0.7} - F \right] W_j^{0.7} \qquad - (10)$$

For this integration simple forward differences are used

$$W_{j,\,n+1} = W_{j,n} + \left[h. \; 0.7(1-E) \; \Sigma \, GR_n / \Sigma \, Z_{j,n} \, W_{j,n}^{0.7} - F \right] W_{j,n}^{0.7}$$

Zooplankton reproduction

It is assumed that the copepods grow from an initial weight W0 to a final weight W2. When this weight is reached, food assimilated is converted into eggs following the same metabolic pattern as occurred for growth.

If S_j is the quantity of egg material then, for $W_j = W2$

$$\frac{dSj}{dt} = (0.7(1-E)h \; \Sigma \, GR_n / \Sigma \, Z_j \, W2^{0.7} - F) \, W2^{0.7}$$

for $0 \leqslant L_j \leqslant LO$

where L_j = number of days after $W_j = W2$.

When $L_j = LO$ a fraction, X, of the accumulated egg material is transformed into juveniles with weight WO. This fraction, X, will depend on metabolic losses by the eggs during development, and on mortality. It is assumed that there is no density dependent mortality during this period although earlier studies suggest this may be an important factor in the ecosystem. The juveniles are also supposed to be of the same age and weight, and to start feeding, at $L_j = LO$. This artificiality is necessary to maintain the cohort structure.

The number of new members of the cohort is given by

$$Z_j = X \; S_j / WO$$

At the end of this reproductive phase some adults will be left. These numbers are usually small and they are put in a separate category, Y_j. They are eliminated by a simple mortality relation,

$$\frac{dYj}{dt} = G. \, Y_j \, W2/(H + W2). \quad \text{(see next section)}$$

Zooplankton mortality

The description of a suitable functional relation for predation on the zooplankton is the most difficult part of this model.
It is assumed that the mortality of each cohort is independent of numbers in other cohorts and is a function of weight and of numbers in the cohort. This assumes that predators are size specific. Within this specific size, however, numbers will still be relevant. Again, the simplest general form is a hyperbolic type of relation. Two relations are available, one depending on biomass (W.Z) and one on numbers (Z).

$$\frac{dZj}{dt} = -G(W_j - DE)(Z_j - DF)/(H + W_j) - GX(Z_j - DF)/(HX + Z_j)$$

This allows a wide range of responses to be simulated involving various threshold effects (DE, DF, G, GX, H and HX are constants). This is solved by simple forward differences.
The post-reproductive adults are removed by using only the first term with DE = DF = 0.
In the earlier equation (7), for completeness, a term

$$\sum_{j=1}^{b} Y_j \, W2^{0.7}$$

is added into the simulation to take account of the grazing of these animals.

This completes the description of the system of equations and numerical methods used to represent the planktonic ecosystem. The following sections describe the simulation in more detail.
The program, written in Fortran II, is given in Appendix II.

Variables and Coefficients

As a summary of the model developed here, and as an indication of the large number of parameters which must be defined, the input to the model is listed below.

Subscripted variables
ee DIMENSION statements — lines 1 to 3 in Appendix II)

1. IB(N) is the total biomass for day N.
2. IP(N) is the phytoplankton carbon for day N in the surface layer.
3. JN (I, J) is the average nitrogen value in layer J $1 \leqslant J \leqslant 12$
4. JC (I, J) is the average phytoplankton carbon in layer J $1 \leqslant J \leqslant 12$
5. PH(I); photosynthetic rate as a function of light. This is input to the model as an average for each layer, I (I = 2 — 13).
6. DIF(I) defines the vertical diffusivity between the I — 1 and the I^{th} layer. This is input to the model.
7. P(I) is the average phytoplankton carbon (mg/m^3) at any time (T).
8. PX(I) is P(I) at the previous time interval (T—1). This is required to be held over from the previous step for the Du Fort-Frankel calculation.
9. R(I) is the average nitrogen. Within the model this is expressed as the carbon equivalent using a C/N ratio of 7:1.
10. RX(I) is R(I) at T—1 (see 8).
11. PN(I) is P(I) at T+1 (again this is a computational requirement).
12. RN(I) is R(I) at T+1 (as 11).
13. W(J) is the weight of an individual copepod (μgC) of the j^{th} cohort.

14. Z(J) is the number of copepods under $1m^2$. Number is expressed as $X10^{-3}$ so that ZW is in mgC.
15. Y(J) is number of post reproductive adults.
16. S(J) is the reproductive material produced by the adults since they reached adulthood (W2).
17. L(J) is the number of days of adult life since they reached the weight W2.
18. PROD(I) is PR_m.
19. GRAZ(I) is GR_m.
20. SINK(I) is the sinking term in the equation for P_m.
21. BASL(I) is the basal metabolism (BA_m) in the equation for EX_m.
[18-21 are required to shorten the length of the equations for *P* and *R*]

READ (3) instruction (line 6 in Appendix II)

ITIME = length of time for which run lasts

Usually, ITIME = 301 but it can go up to 2501.

MULT = interval (in days) of output of JN and JC values for plotting N and C profiles. If ITIME = 301, MULT is usually = 10. However, if ITIME = 2501, MULT ⟩ 25.

Coefficients
[READ (1) statements, lines 9 and 10 in Appendix II]

1. *KKK;* an integer taking value 1 or 2. If *KKK* = 2 then only one set of input parameters PH(I), DIF(I) is read in at the beginning so that photosynthetic rate and diffusion are constant throughout the run. If *KKK* = 1 then a new set is read in each day.
2. *M* is the number of days for which the FD system is used; after M days the program goes to DFF.
3. *A* is the half-saturation constant (k_s) of the nutrient equation. The V_{max} is included in the PH term). Units are mgC/m^3.
4. *B* has a value between 0 and 1. It defines the vertical distribution of the zooplankton.
5. *C, D* define the relation of grazing to phytoplankton concentration (roughly equivalent to V_{max} and k_s in the nutrient kinetics) $C \sim day^{-1}$; $D \sim mgC/m^3$.
6. *E* the fraction of assimilated food which is lost on conversion to body substance (a form of specific dynamic action).
7. *F* is a coefficient for basal metabolism ($F.W^{0.7}$) independent of food intake ($F \sim day^{-1}$).
8. *PO* is the threshold concentration of phytoplankton below which zooplankton feeding ceases ($PO \sim mgC/m^3$).
9. *RMAX* is the concentration of nutrients in the water above which phytoplankton in this water have neutral buoyancy ($RMAX \sim mgC/m^3$)
10. *V* is the maximum sinking rate of phytoplankton achieved at R = 0 ($V \sim m/day$).
11. LO is the period of time during which the food intake of adult copepods goes to reproduction. The new cohort starts feeding at the end of this period (LO ∼ days).
12. *X* is the fraction of energy put into eggs which reappears as nauplii. This combines both respiratory losses and mortality.
13. *G, H* are coefficients for predation on zooplankton *biomass* (Z.W) ($G \sim 10^{-3}$ number/m^2/day. $H \sim mgC/m^2$).
14. *DE* is the threshold for weight of a copepod below which there is no predation (μgC).

15. *GX, HX* are coefficients for predation on zooplankton *numbers* (Z) (GX $\sim 10^{-3}$ numbers/m^2/day; HX $\sim 10^{-3}$ numbers/m^2.
16. *DF* is the threshold below which predation on zooplankton numbers is zero (DF $\sim 10^{-3}$ numbers/m^2).
17. *WO* is the initial weight of a copepod, i.e. the weight at which it starts feeding (μgC).
18. *W2* is the final weight of a copepod, i.e. weight of the adult (μgC).
19. *RESP* is the respiration rate of phytoplankton expressed as fraction of carbon utilised per day.
20. *DELZ* is the depth interval over which properties are averaged (m).
21. *ADDR* is the daily rate of addition of nutrient R to the bottom layer (in equivalent carbon units). This is intended to simulate the rate of release of nutrient from the bottom, or the addition of nutrient to a bag (mgC/m^3).

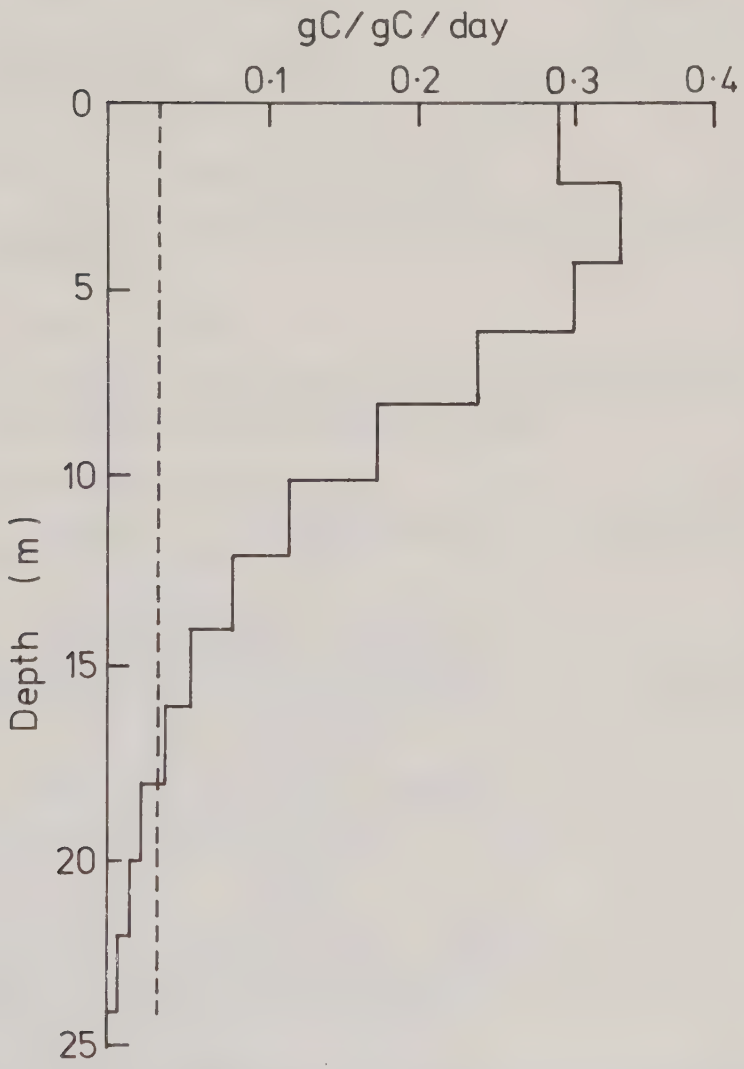

Figure 2. Depth distribution of photosynthesis (g C/phytoplankton C/day) with the rate of respiration shown by a dashed line.

Numerical values used for basic run

PH, DIF and initital conditions

1. PH(I) see Figure 2; in other runs x ½, x 2 are used as tests.
2. DIF(I) numerical value of 5 at all depths ≡ 0.6 cm^2/sec. In other runs values of 2, 10 and 20 are used.
3. P(I) = 300 mgC/m^3 is the initial value at all depths.

4. R(I) = 3 mg at N/m^3 is the initial value at all depths.
(In other runs P/R values of 500/1.00 and 100/5.00 are used).
Initial values for the zooplankton are:

		(1)	(2)	(3)	(4)	(5)	(6)
5. W(J)	=	0.2	2.0	10	30	70	101 μgC
6. Z(J)	=	50	30	5	2	1	0.2 $\times 10^3$
7. S(J)	=	0	0	0	0	0	50 μgC
8. L(J)	=	0	0	0	0	0	10 days

(This assumes the copepod to be of the *"Calanus"* type. The last cohort takes 10 days to pass through its reproductive life during which it accumulates 50 μgC reproductive material).

Coefficients

1. KKK = 2;i.e. DIF and PH are constant with time.
2. A = 1 mg at N/m^3 is the half saturation value for nitrogen kinetics.
3. B = 1; i.e. grazing is equal at all depths.
4. C = 2/day; D = 200 mgC/m^3 ; D is the "half-saturation" value.
To interpret C, the daily carbon intake by a copepod with average food concentration P is

$$W^{0.7}\, C\, (P - PO)/(D + P - PO)$$

(PO = 50, see (7))

For a 100μgC copepod this is approximately 21μgC/day at P = 200.
For a 1μgC copepod the value is 0.86μgC/day.

5. E = 0.4 i.e. 60% of assimilated food is available for growth and basal metabolism.
6. F = 0.1 is the coefficient for basal metabolism, e.g. for a 100μgC animal, $F.W^{0.7}$ = 2.5μgC goes to basal metabolism daily.
[In summary a 100μgC copepod (at P = 200) would eat 21μgC, assimilate 14.7μgC, convert 8.8μgC, lose 2.5 as basal metabolism, leaving approximately 6μgC for growth, per day]
7. PO = 50 mgC/m^3 is the threshold feeding level.
8. RMAX= 5 mg at N/m^3 is the nutrient concentration for zero sinking.
9. V = 0.2 m/day is the maximum sinking rate.
10. LO = 20 days is the duration of reproduction.
11. X = 0.1 i.e. 10% of food intake by adults ends up as nauplii.
12. G = 3, H = 1000 in the predation relation.
Since W $\ll$ 100, this means that, effectively, daily loss of animals = .003 W.Z i.e. rate of predation depends on biomass.
13. DE = 0 i.e. no threshold weight in predation.
14. In the basic run GX = HX = 0 i.e. predation on numbers alone is not used.
15. DF = .05 a very low threshold on numbers is used.
16. WO = 0.2μgC is the initial weight of a nauplius.
17. W2 = 100μgC assumed to be the weight of a *Calanus*.
18. RESP = 0.03μgC/ μgC/day for phytoplankton (see Fig. 1).
19. DELZ= 2.0m giving total depth of 24m. (This simulation is intended for studies with large plastic enclosures).
20. ADDR= .5 mg at/m^3 /day in the bottom layer. Since the layer is 2m thick this is a release from the bottom of 1 mg at/m^2/day.

TABLE I Output from model

Day	N(1)	N(2)										N(12)	$\bar{N}$
	P(1)	P(2)										P(12)	$\bar{P}$
	Z(1)	Z(2)				Z(6)	W(1)					W (6)	BIOM
0	300	300	300	300	300	300	300	300	300	300	300	300	3.00
	300	300	300	300	300	300	300	300	300	300	300	300	300
	50.0	30.0	5.0	2.0	1.0	0.2	0.2	2.0	10.0	30.0	70.0	101.0	.270
1	241	238	244	256	269	282	291	298	303	308	319	342	2.83
	344	353	350	340	326	314	304	297	293	290	288	287	315
	50.0	29.8	4.8	1.8	0.8	0.2	0.3	2.7	12.0	34.2	77.5	101.0	.297
2	182	185	194	213	236	259	278	294	307	321	341	369	2.65
	395	398	393	377	355	333	314	299	289	282	279	277	333
	49.9	29.5	4.7	1.6	0.7	0.1	0.5	3.5	14.2	38.9	85.8	101.0	.331
3	129	133	148	173	204	236	265	290	311	333	358	391	2.48
	437	442	433	413	384	353	325	303	287	277	270	267	349
	49.8	29.2	4.5	1.5	0.5	0.1	0.8	4.5	16.9	44.2	94.9	101.0	.375
4	84	91	107	137	174	214	252	285	314	343	373	408	2.32
	469	474	467	443	410	372	337	309	287	272	263	259	363
	49.7	28.8	4.2	1.3	0.4	0.1	1.2	5.7	19.9	50.0	100.8	101.0	.426
5	54	60	77	108	149	195	239	280	317	351	386	423	2.20
	486	495	488	466	430	390	349	315	288	269	257	251	374
	49.4	28.2	4.0	1.1	0.3	0.1	1.8	7.2	23.4	56.5	100.8	101.0	.487
6	36	41	58	88	130	179	228	275	318	358	396	435	2.12
	491	500	498	478	445	403	359	320	289	266	252	244	379
	49.1	27.6	3.7	0.9	0.3	0.1	2.4	8.9	27.3	63.7	100.8	101.0	.560
7	28	32	47	75	116	166	220	271	319	363	405	446	2.08
	485	497	498	483	452	411	366	325	290	264	247	239	380
8	24	28	41	68	108	158	213	268	320	368	412	455	2.06
	474	488	492	480	453	414	370	327	290	261	243	233	377
	48.2	25.9	3.1	0.6	0.2	0.1	4.3	13.3	36.4	79.9	100.8	101.0	.737
9	23	26	39	64	103	153	210	267	321	372	419	462	2.05
	461	476	481	473	449	413	369	326	288	258	238	228	372
	47.5	24.8	2.8	0.5	0.1	0.1	5.5	15.9	41.7	88.9	100.8	101.0	.337
10	23	26	38	63	101	151	208	267	323	376	424	468	2.06
	447	461	468	462	442	407	366	323	284	254	233	222	364
	46.7	23.6	2.4	0.4	0.1	10.1	6.9	18.8	47.4	98.6	100.8	0.2	.943

Presentation

The model is run for 300 days so that general trends can be seen. A printed output (Table I) gives the daily values of (1) nutrients and plant carbon in each layer (2) numbers and weight of animals in each cohort, (3) average nutrients and plant carbon over the water column and (4) total biomass of animals. All these can be plotted by a plotter program. The N and P are plotted against depth at 10-day intervals. The zooplankton numbers and weights are plotted on a log scale so that each cohort can be followed. The values of N and P at any depth can be plotted as can the total biomass.

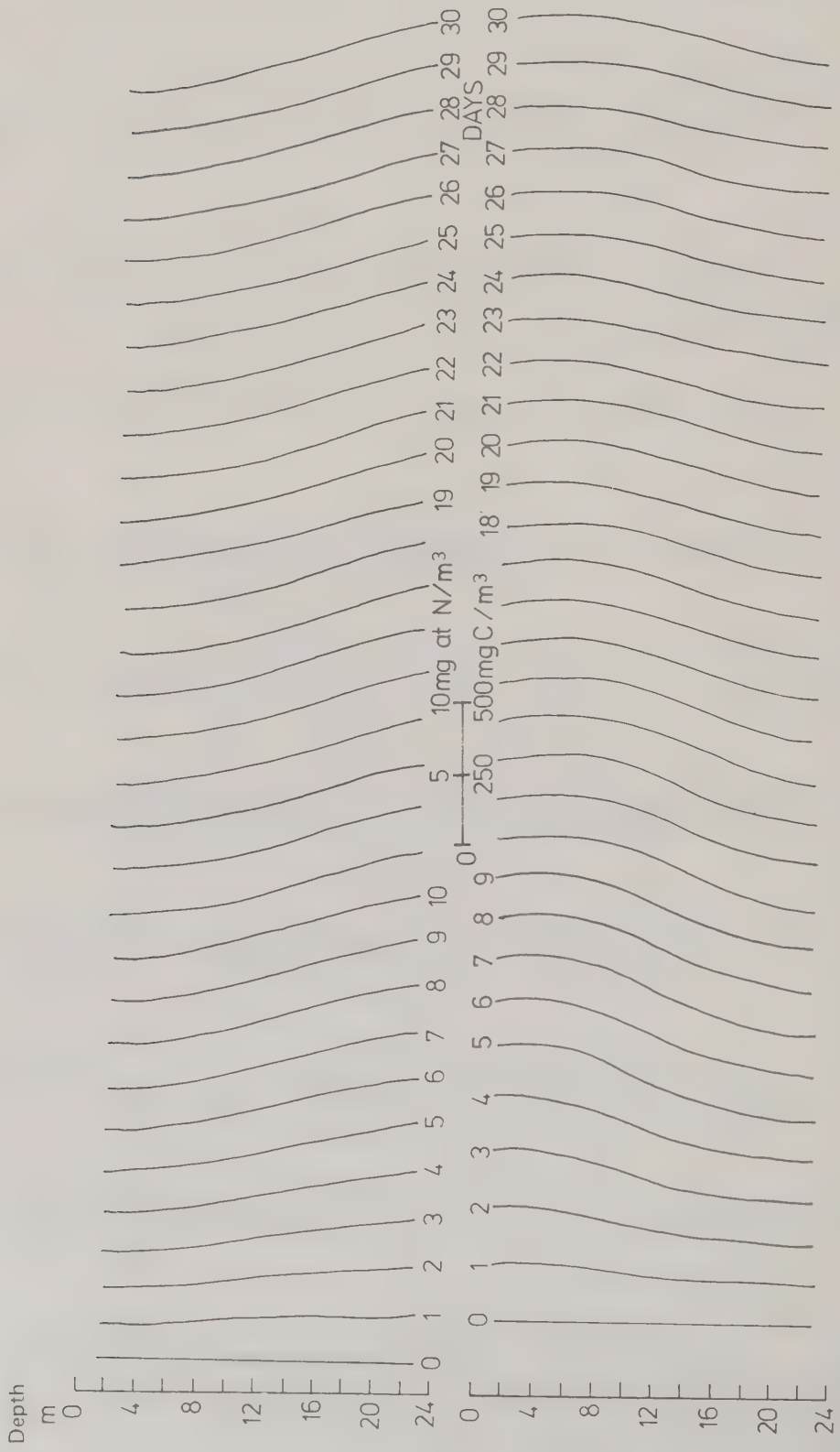

Figure 3. Vertical profiles of *N* (as mg at/m³) and *P* (as mg C/m³) at one day intervals for the first 30 days.

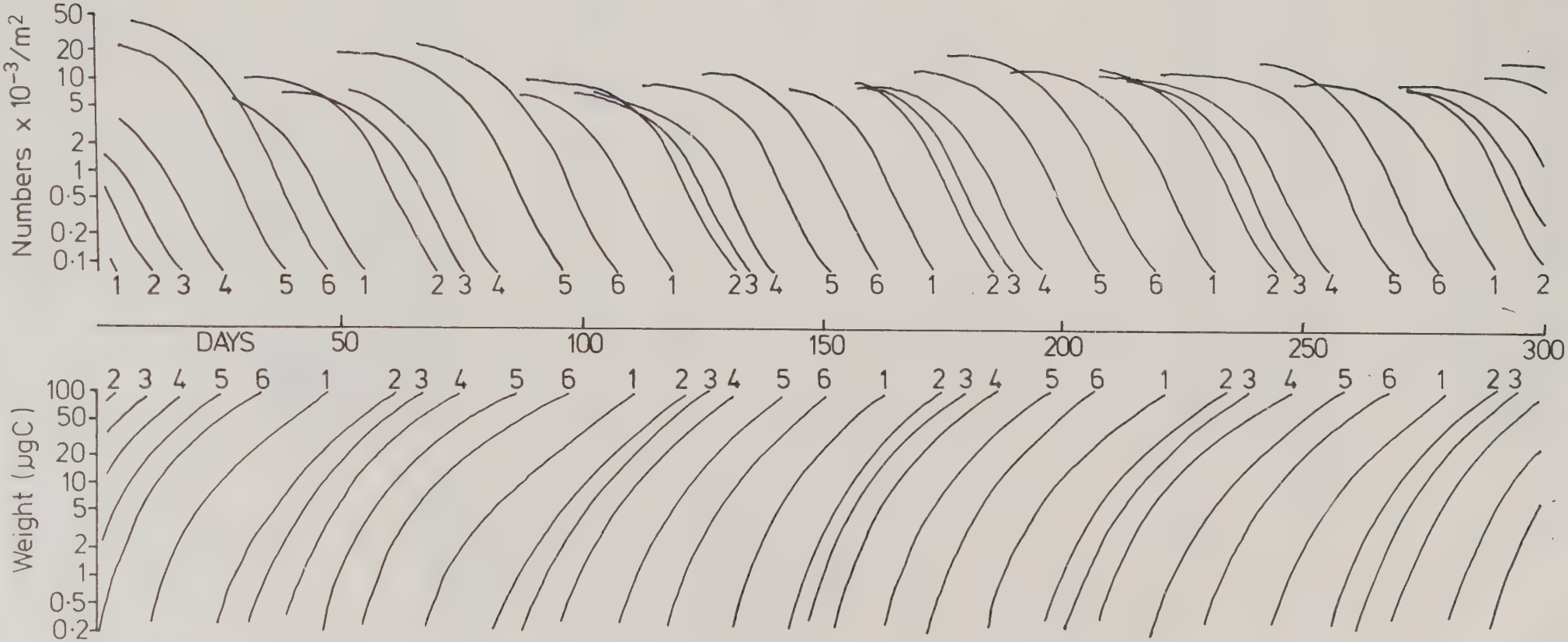

Figure 4. Numbers (*Z*) and weights (*W*) of six cohorts of a herbivorous copepod grazing on *P.*

Test runs

(1) Nutrient and plant carbon as functions of depth. Figure 3 shows the basic run with smooth curves resulting from a constant mixing rate between all layers.
(2) Zooplankton numbers and weight, Figure 4 shows the changes for each cohort where, essentially

$$\frac{dZ}{dt} = .003\ W.Z.$$

(3) Changes in plant and animal biomass. The best way to summarise the changes in zooplankton is in terms of the total biomass (Σ WZ) expressed as gC/m^2.

Similarly for phytoplankton the changes in carbon in the surface layer are a good index. Figure 5 shows these for the basic run.

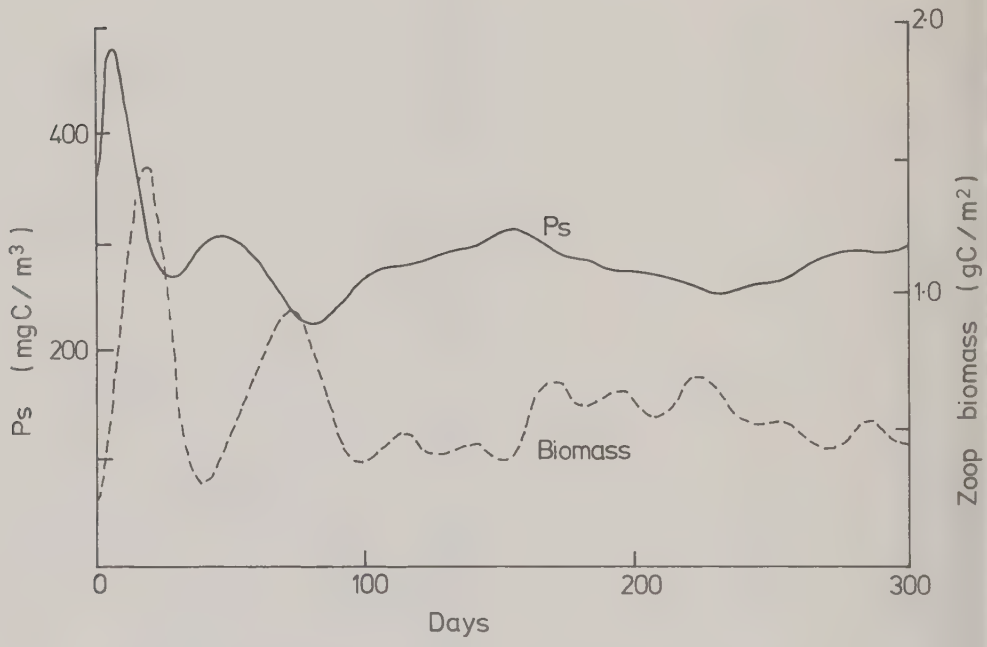

Figure 5. Surface phytoplankton concentrations, P_s, and zooplankton biomass, BIOM, for C = 2, D = 200, PO=50.

Flow Diagram

These are two main cycles in the program (Figure 6) DO21 defines a daily loop which includes the PRINT/PLOT of the results. An internal loop based on IF(LLL-INVT) takes the main computation of R, P, W and Z through INVT cycles per day. The choice of FD or DFF for the computation of R and P depends on IF(N-M-1).

The calculation of Z and W is carried out by DO80 and a separate flow diagram (Figure 7) is given for this.

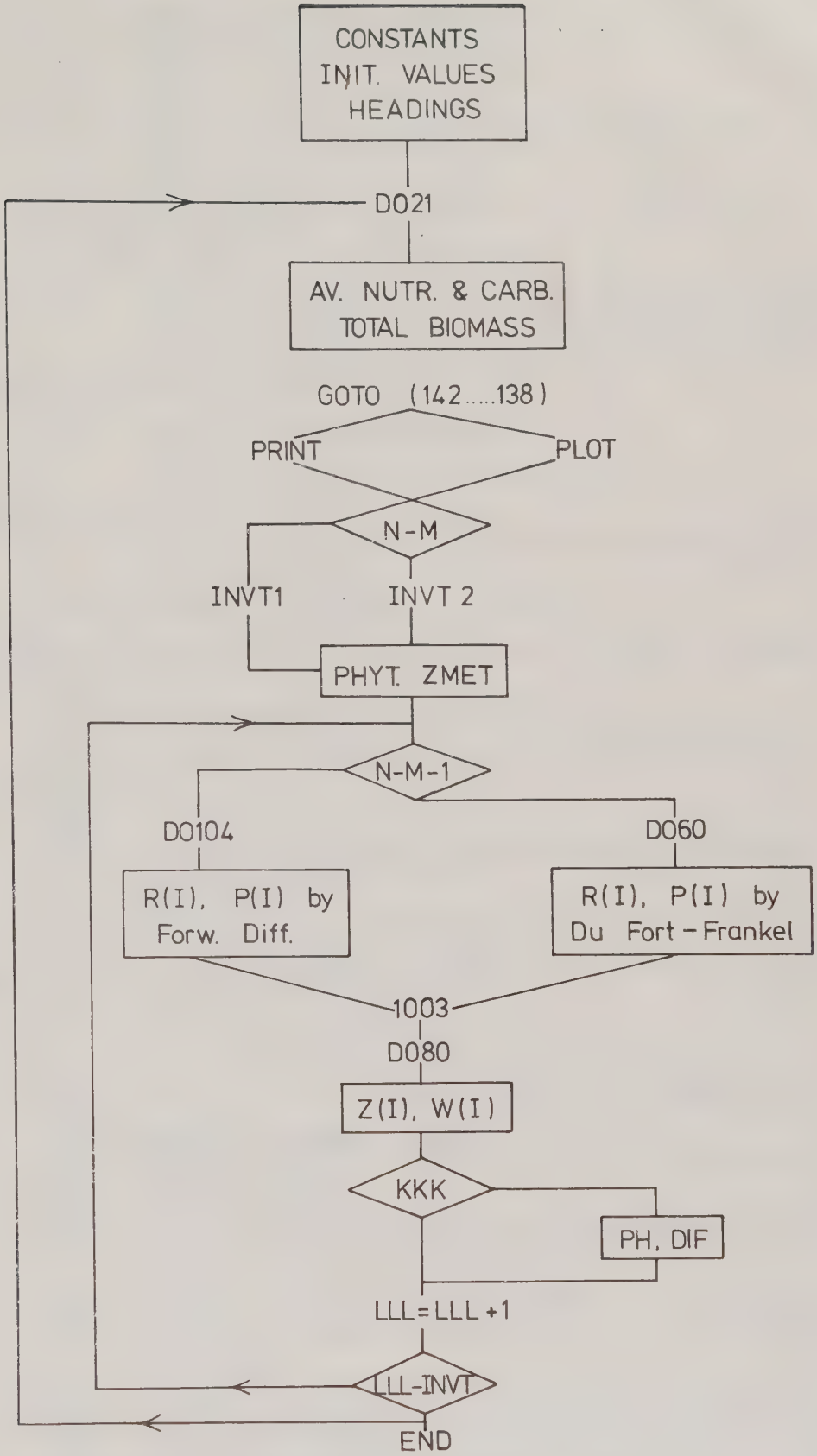

Figure 6. Flow diagram of program.

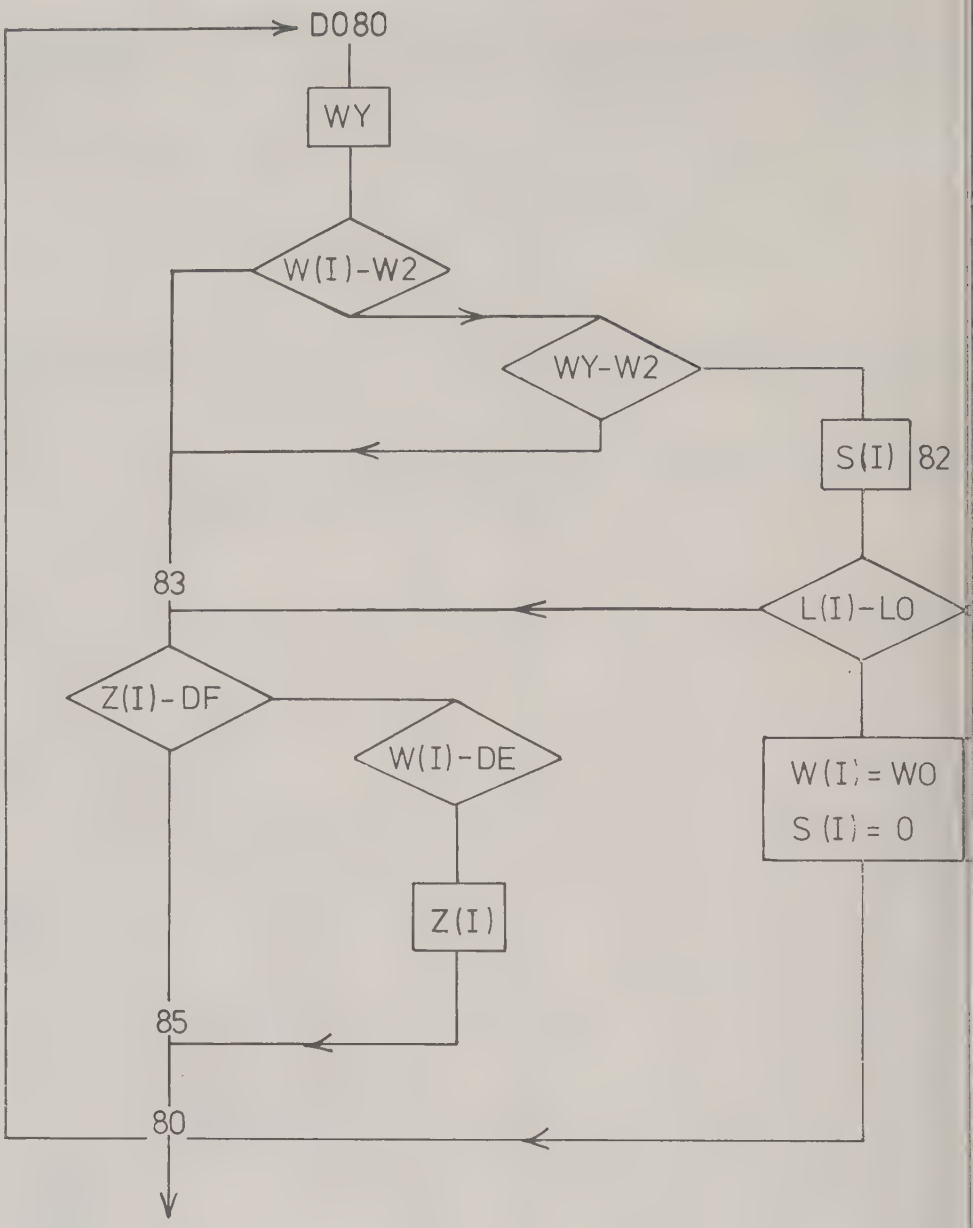

Figure 7. DO80 loop for calculation of Z, W.

Statement Lists

2-6	See pp. 9 - 11 for listing of variables.
8-10	See pp. 9 - 11 for listing of constants.
11-13	Sets IB and IP locations to zero.
14	INT is used to count the days that have been cycled in the program.
16-17	Read in initial values of R & P for 12 depth intervals (I = 2,13 is used so that $R_{-1} = R(1)$).
18-22	Values of R, P outside the boundaries are set to zero.
24-26	Read in initial values of W, Z and of L, S which allow some of the zooplankton population to be adults at various stages of reproduction. Y(J) =0 assumes there are no post-reproductive adults.
28-30	Write headings for print out.
32-33	Read in initial values for PH and DIF.
35	This is the main cycle for the whole program.
36	IDAY for print out starts at N-1.
37	ANUTR is the average R in the water column (for print out).
38	CARB is the average P " " " " " " "
39	BIOM is the total biomass of zooplankton.
40	LLL is used for the internal cycle over the number of time steps (INVT) per day (see 210-211).
42-47	Calculates ANUTR, CARB and BIOM for print out.
48	Increments the daily count each time it goes through the main loop.
50-61	Print out.
63-64	Store the total biomass and surface phytoplankton values after scaling them.
66-77	Do the cycle to store N & C values for plotter every MULT days.
78-82	If N $\langle$ M, the program is used with INVT1 cycles per day. If N $\rangle$ M then INVT2 cycles per day is used.
83	DELT is the time step in "day" units.
84	DEL is "k/h^2" associated with the diffusion terms.
85 and 89-90	PHYT ($= \Sigma P_i$) is used in describing the vertical distribution of grazing
86 and 92-93	ZMET ($= \Sigma Z_j W_j^{0.7} + \Sigma Y_j W2^{0.7}$) is used in the terms for zooplankton metabolism.
87 and 102	TGRA is the total quantity of phytoplankton grazed per unit time, derived by summing grazing in each layer.
95-96	PROD(I) is the phytoplankton production.
97-101	GRAZ(I) is the grazing per unit volume in each layer. This is zero if P(I) $\langle$ PO.
104	BASL(I) is the "basal" metabolism derived from the coefficient *F*.
105	This determines whether FD or DFF is used for R & P.
107-116	This loop determines the new R and P as RN(I) and PN(I) by FD.
108-112	Calculates the sinking term.
117-121	This loop updates R(I) and P(I). Strictly, for FD, there is no need to have the three time levels (e.g. RX, R, RN) but these are required at the final time step when the program goes to DFF and so it is easiest to carry them throughout.
122	This adds in the nutrients in the lowest layer.
123	After FD the program goes to zooplankton calculations.

125-141 This is the loop for DFF to calculate R and P for all the *internal* points, i.e. I = 3-12. PROD, GRAZ & BASL are averaged from I+1, I-1.

142-145 For calculation of the boundary values, the values of R and P at positions 1 and 14 outside the boundaries are determined.

146-147 The "outside" values of PH.

149-172 Repeats the calculations in 125-141 for the boundary points except that SINK (2) and SINK (13) are calculated separately.

173-177 Updates RX, R,PX and P.

179 Adds in the nutrient to the bottom layer.

182-205 Main loop for zooplankton (see Fig. 2).

183 WY is a dummy variable, finally used for updating at 204.

184-185 If W(I) and WY are both greater than or equal to W2, then WY-W(I), the apparent increase in weight, actually goes to reproduction S(I). Otherwise WY is used for growth (204).

187 This calculates the increase in S(I) and

188 WY is left equal to W(I).

190 Updates the time spent in the reproductive phase.

191 Determines if the end of the reproductive phase has been reached.

192 Sets the weight W(I) back to the initial weight WO.

193 Any animals left are put in a separate category Y(I) with a separate mortality rate (at 205).

195 The numbers of this new generation are calculated from the amount of reproductive material produced by the adults.

196-197 L(I) and S(I) are set at zero for the new cohort.

199-200 Determine if Z(I) and W(I) are above the threshold values. If they are below these, then there is no predation.

201-203 Determine the predation by the two functions (see text).

206-209 KKK is used to determine whether the same PH and DIF values are used throughout the run or whether they are updated at each time step.

210-211 IF (LLL-INVT) determines whether the program cycles through the print or only through the time advance steps.

214 Input of a dummy variable (NODDY). Gives the operator time to run out (or reload) the punch prior to

216-227 the output of the MANY values of JN and JC which are the nitrogen and phytoplankton values at each of the 12 depth intervals. These are required for later plotting by NCPROF.

228 A counter to check the state of the P_s and BIOM plot.

230 LOP2 = 0 ⇒ NO P_s & BIOM plot is required.

= 1 ⇒ P_s & BIOM plot is required.

II = 5 ⇒ each day is represented on the horizontal axis by 5 plotter units (P.Us) i.e. by 0.05 cm. II = 5 is used if ITIME = 301. However, if ITIME = 2501, the operator must set II = 1 i.e. 1 day = 1PU = 0.01 cm.

231-232 Check sequence to determine if plot is required.

233 BIOM and P_s scaling factors

FACB = 1 ⇒ 0.1 on BIOM scale = 0.5 cm

FACP = 1 ⇒ 100 on P_s scale = 2.0 cm

234-237 Scales the BIOM & P_s values held in store by FACB and FACP respectively.

238 Sets the time increment.

240-242 Sets the pen at the origin at a suitable distance in from the lefthand edge.

246-250 Draws the horizontal and vertical axes.

251 Sets the pen at the first BIOM value.

252-255 Draws the BIOM curve.

256-257 Reminds the operator (via teleprinter) to change the plotter pen if necessary.

258 Input of a dummy variable to enable operator to perform previous step before the program continues.

259 Sends pen back to origin.

260-261 Checks to see whether one or both plots have been done.

262-263 Replaces the BIOM values in store by the P_s values.

264 Resets time increment.

265 Transfers control to 211 to enable P_s curve to be drawn.

Summary

A simulation model is given which describes changes with time and depth in nutrients, phytoplankton and zooplankton.

References

Davies, J.M., Gamble, J.C. and Steele, J.H. 1975. Preliminary studies with a large plastic enclosure. In *Cronin, L.E. ed. Estuarine Research Vol. 1.* New York, Academic Press. 251-264.

Du Fort, E.C. and Frankel, S.P. 1953. Stability conditions in the numercial treatment of parabolic differential equations. *Mathl Tabl. natn. Res. Coun., Wash.* **7** (43), 135-152.

Steele, J.H. 1962. Environmental control of photosynthesis in the sea. *Limnol. Oceanogr.* **7**, 137-150.

Steele, J.H. and Yentsch, C.S. 1960. The vertical distribution of chlorophyll. *J. mar. biol. Ass. U.K.* **39**, 217-226.

Steele, J.H. and Baird, I.E. 1972. Sedimentation of organic matter in a Scottish sea loch. *Memorie 1st. ital. Idrobiol.* **29** (Suppl.), 73-88.

APPENDIX I Initial Parameters

ITIME MULT

KKK M A B C D E F PO RMAX V LO X

G H DE GX HX DF WO W2 RESP DELZ INVTI INVT2 ADD

R(2) → R(13)

P(2) → P(13)

W(1) → W(6)

Z(1) → Z(6)

L(1) → L(6)

S(1) → S(6)

PH(2) → PH(13)

DIF(2) → DIF(13)

LOP2 II

FACB FACP

```
GLOBAL,BAGK,PLOTTER]
DIMENSION IB(2501),IP(2501),JN(101,12),JC(101,12)
DIMENSION PH(14),DIF(14),P(14),PX(14),R(14),RX(14),PN(14),RN(14)
DIMENSION W(6),Z(6),Y(6),S(6),L(6),PROD(14),GRAZ(14),SINK(14),BASL(14)
COMMON PH,DIF,P,PX,R,RX,PN,RN,W,Z,Y,S,L,PROD,GRAZ,SINK,BASL
COMMON IB,IP,JN,JC
C   INPUT INITIAL DATA
READ(3)ITIME,MULT
READ(1)KKK,M,A,B,C,D,E,F,PO,RMAX,V,LO,X
READ(1)G,H,DE,GX,HX,DF,WO,W2,RESP,DELZ,INVT1,INVT2,ADDR
DO 9999 N=1,ITIME
IB(N)=0
9999 IP(N)=0
INT=-1
C   INPUT INITIAL NUTRIENT AND PHYTOPLANKTON VALUES
DO 10 I=2,13

10 READ(1)R(I),P(I)
R(1)=0.0
R(14)=0.0
P(1)=0.0
P(14)=0.0
DIF(14)=0.0
C   INPUT INITIAL ZOOPLANKTON VALUES
DO 11 J=1,6
READ(1)W(J),Z(J),L(J),S(J)
11 Y(J)=0.0
C   OUTPUT HEADINGS
WRITE(1,12)
12 FORMAT(3HDAY,2X,3H(1),2X,3H(2),2X,3H(3),2X,3H(4),2X,3H(5),2X,3H(6),
$ 2X,3H(7),2X,3H(8),2X,3H(9),2X,4H(10),2X,4H(11),2X,4H(12))
C   INPUT INITIAL PHOTOSYNTHETIC AND VERTICAL DIFFUSIVITY RATES
DO 13 I=2,13
13 READ(1)PH(I),DIF(I)
C   START MAIN PROGRAM LOOP
DO 21 N=1,ITIME
IDAY=N-1
ANUTR=0.0
CARB=0.0
BIOM=0.0
LLL=1
C   CALCULATE AVERAGE NUTRIENTS AND PLANT CARBON IN WATER COLUMN
DO 14 I=2,13
ANUTR=ANUTR+R(I)*0.01/12.0
14 CARB=CARB+P(I)/12.0
C   CALULATE TOTAL ZOOPLANKTON BIOMASS IN WATER COLUMN
DO 15 K=1,6
15 BIOM=BIOM+(W(K)*Z(K)+W2*Y(K))/10**3
INT=INT+1
C   OUTPUT ROUTINE
142 WRITE(1,22)IDAY,R(2),R(3),R(4),R(5),R(6),R(7),R(8),R(9),R(10),R(11),R(12),R(13)
22 FORMAT(I3,12I6)
WRITE(1,16)ANUTR
16 FORMAT(Z,2X,F4.2)
WRITE(1,27)P(2),P(3),P(4),P(5),P(6),P(7),P(8),P(9),P(10),P(11),P(12),P(13)
27 FORMAT(3X,12I6)
WRITE(1,17)CARB
17 FORMAT(Z,2X,I5)
WRITE(1,28)Z(1),Z(2),Z(3),Z(4),Z(5),Z(6),W(1),W(2),W(3),W(4),W(5),W(6)
28 FORMAT(3X,12F6.1)
WRITE(1,18)BIOM
18 FORMAT(Z,2X,F5.3)
```

```
C   SCALING AND STORAGE OF BIOMASS AND SURFACE PLANT CARBON VALUES
IB(N)=BIOM*500.
IP(N)=P(2)*2.
C   SCALING AND STORAGE OF NUTRIENT AND PLANT CARBON VALUES
1270 IF(IDAY)1280,1280,1320
1280 NUMB=0
1288 INT=0
NUMB=NUMB+1
DO 1290 I=2,13
KMT=I-1
1290 JN(NUMB,KMT)=R(I)
DO 1370 I=2,13
KMT=I-1
1370 JC(NUMB,KMT)=P(I)*2.0
GO TO 46
1320 IF(INT-MULT)46,1288,1288
46 IF(N-M)201,201,202
201 INVT=INVT1
GO TO 203
202 INVT=INVT2
203 CONTINUE
DELT=1.0/INVT
DEL=DELT/(DELZ**2)
PHYT=0.0
ZMET=0.0
TGRA=0.0
C   TOTAL PLANT CARBON
DO 40 I=2,13
40 PHYT=PHYT+P(I)
C   ZOOPLANKTON METABOLISM
DO 41 I=1,6
41 ZMET=ZMET+Z(I)*W(I)**0.7+Y(I)*W2**0.7
C   PHYTOPLANKTON PRODUCTION
DO 50 I=2,13
PROD(I)=(PH(I)*R(I)/(A+R(I))-RESP)*P(I)
IF(P(I)-PO)51,51,52
51 GRAZ(I)=0.0
GO TO 53
C   ZOOPLANKTON GRAZING
52 GRAZ(I)=ZMET*(B/12.+(1-B)*P(I)/PHYT)*C*(P(I)-PO)/(D+P(I)-PO)/DELZ
53 TGRA=TGRA+GRAZ(I)*DELZ
C   ZOOPLANKTON METABOLISM
50 BASL(I)=F*ZMET*(B/12.+(1-B)*P(I)/PHYT)/DELZ
IF(N-M-1)54,54,55
C   FORWARD DIFFERENCE
54 DO 104 I=2,13
IF(R(I)-RMAX)101,102,102
102 SINK(I)=0.0
GO TO 103
C   SINKING OF PHYTOPLANKTON
101 SINK(I)=V*(P(I-1)*(1-R(I-1)/RMAX)-P(I)*(1-R(I)/RMAX))/DELZ
C   NUTRIENTS AT TIME T+1
103 RN(I)=R(I)+(0.7*E*GRAZ(I)+BASL(I)-PROD(I))*DELT+DEL*(DIF(I+1)*(R(I+1)-R(I))-DIF(I)*(R(I)-R(I-1)))
C   PLANT CARBON AT TIME T+1
104 PN(I)=P(I)+(PROD(I)-GRAZ(I)+SINK(I))*DELT+DEL*(DIF(I+1)*(P(I+1)-P(I))-DIF(I)*(P(I)-P(I-1)))
DO 10002 I=2,13
RX(I)=R(I)
PX(I)=P(I)
R(I)=RN(I)
10002 P(I)=PN(I)
R(13)=R(13)+ADDR/INVT
GO TO 10003
C   DU-FORT FRANKEL
```

```
55 DO 60 I=3,12
IF(R(I)-RMAX)61,62,62
62 SINK(I)=0.0
GO TO 63
C   SINKING OF PHYTOPLANKTON
61 SINK(I)=V*(P(I-1)*(1-R(I-1)/RMAX)-P(I+1)*(1-R(I+1)/RMAX))/DELZ
C   PHYTOPLANKTON PRODUCTION
63 PRO=PROD(I+1)+PROD(I-1)
C   ZOOPLANKTON GRAZING
GRA=GRAZ(I+1)+GRAZ(I-1)
C   ZOOPLANKTON METABOLISM
BAS=BASL(I+1)+BASL(I-1)
DEZ=1.+(DIF(I+1)+DIF(I))*DEL
C   NUTRIENTS AT TIME T+1
RN(I)=((0.7*E*GRA+BAS-PRO)*DELT+2.*(DIF(I+1)*R(I+1)+DIF(I)*R(I-1))*DEL+(1-(DIF(I+1)+DIF(I))*DEL)*RX(I))/DEZ
C   PLANT CARBON AT TIME T+1
60 PN(I)=((PRO-GRA+SINK(I))*DELT+2.*(DIF(I+1)*P(I+1)+DIF(I)*P(I-1))*DEL+(1-(DIF(I+1)+DIF(I))*DEL)*PX(I))/DEZ
R(1)=2*RX(2)+RN(4)-RX(4)-R(3)
P(1)=2*PX(2)+PN(4)-PX(4)-P(3)
R(14)=2*RX(13)+RN(11)-RX(11)-R(12)
P(14)=2*PX(13)+PN(11)-PX(11)-P(12)
PH(1)=2*PH(2)-PH(3)
PH(14)=2*PH(13)-PH(12)
C   SINKING OF PHYTOPLANKTON AT UPPER BOUNDARY
IF(R(2)-RMAX)70,71,71
70 SINK(2)=-V*P(3)*(1-R(3)/RMAX)/DELZ
GO TO 301
71 SINK(2)=0.0
C   SINKING OF PHYTOPLANKTON AT LOWER BOUNDARY
301 IF(R(13)-RMAX)72,302,302
72 SINK(13)=V*(P(12)*(1-R(12)/RMAX)-P(14)*(1-R(14)/RMAX))/DELZ
GO TO 73
302 SINK(13)=0.0
C   UPPER AND LOWER BOUNDARY VALUES
73 DO 500 I=1,14,13
PROD(I)=(PH(I)*R(I)/(A+R(I))-RESP)*P(I)
IF(P(I)-PO)510,510,520
510 GRAZ(I)=0.0
GO TO 500
520 GRAZ(I)=ZMET*(B/12.+(1-B)*P(I)/PHYT)*C*(P(I)-PO)/(D+P(I)-PO)/DELZ
500 BASL(I)=F*ZMET*(B/12.+(1-B)*P(I)/PHYT)/DELZ
DO 74 I=2,13,11
PRO=PROD(I+1)+PROD(I-1)
GRA=GRAZ(I+1)+GRAZ(I-1)
BAS=BASL(I+1)+BASL(I-1)
DEZ=1.+(DIF(I+1)+DIF(I))*DEL
RN(I)=((0.7*E*GRA+BAS-PRO)*DELT+2.*(DIF(I+1)*R(I+1)+DIF(I)*R(I-1))*DEL+(1-(DIF(I+1)+DIF(I))*DEL)*RX(I))/DEZ
74 PN(I)=((PRO-GRA+SINK(I))*DELT+2.*(DIF(I+1)*P(I+1)+DIF(I)*P(I-1))*DEL+(1-(DIF(I+1)+DIF(I))*DEL)*PX(I))/DEZ
75 DO 76 I=2,13
RX(I)=R(I)
PX(I)=P(I)
R(I)=RN(I)
76 P(I)=PN(I)
C   RE-INTRODUCTION OF NUTRIENTS TO BOTTOM LAYER
R(13)=R(13)+2.0*ADDR/INVT/DEZ
10003 CONTINUE
C   MAIN LOOP FOR NEW ZOOPLANKTON NUMBERS AND WEIGHTS
DO 80 I=1,6
WY=W(I)+DELT*(0.7*(1.0-E)*TGRA/ZMET-F)*W(I)**0.7
IF(W(I)-W2)83,81,81
81 IF(WY-W2)83,83,82
C   REPRODUCTIVE MATERIAL BY ADULTS
82 S(I)=S(I)+(WY-W(I))*Z(I)
```

```
C   UPDATE OF TIME IN REPRODUCTIVE PHASE
L(I)=L(I)+1
IF(L(I)-(LO*INVT))83,86,86
86 W(I)=WO
Y(I)=Z(I)+Y(I)
C   NUMBERS IN NEW GENERATION
Z(I)=X*S(I)/WO
L(I)=0
S(I)=0
GO TO 80
83 IF(Z(I)-DF)85,85,91
91 IF(W(I)-DE)92,92,93
92 Z(I)=Z(I)-DELT*GX*(Z(I)-DF)/(HX+Z(I))
GO TO 85
93 Z(I)=Z(I)-DELT*(GX*(Z(I)-DF)/(HX+Z(I))+G*(W(I)-DE)*(Z(I)-DF)/(H+W(I)))
85 W(I)=WY
80 Y(I)=Y(I)-DELT*(GX*Y(I)/(HX+Y(I))+G*W2*Y(I)/(H+W2))
IF(KKK-1)94,94,204
C   INPUT OF NEW PHYTOSYNTHETIC AND VERTICAL DIFFUSIVITY RATES IF REQUIRED
94 DO 96 I=2,13
96 READ(1)PH(I),DIF(I)
204 LLL=LLL+1
IF(LLL-INVT)203,203,21
C   END OF MAIN PROGRAM LOOP
21 CONTINUE
READ(3)NODDY
C   OUTPUT OF NUTRIENT AND PLANT CARBON VALUES
DO 1330 NUMB=1,MANY
DO 1340 KMT=1,12
RRA=JN(NUMB,KMT)
1340 WRITE(1,1300)RRA
1300 FORMAT(Z,I5)
WRITE(1,10001)
10001 FORMAT(1X)
DO 1310 KMT=1,12
PPA=JC(NUMB,KMT)
1310 WRITE(1,1300)PPA
WRITE(1,10001)
1330 CONTINUE
KOK=-1
C   PLOT OF BIOMASS AND SURFACE PLANT CARBON IF REQUIRED
READ(3)LOP2,II
IF(LOP2)137,137,126
126 CONTINUE
READ(3)FACB,FACP
DO 127 N=1,ITIME
IB(N)=IB(N)/FACB
IP(N)=IP(N)/FACP
127 CONTINUE
IJ=II
CALL PLOTTER(50)
128 FORMAT(Z,100F50.0)
WRITE(5,128)0,0
WRITE(5,129)0,0
129 FORMAT(X)
130 FORMAT(/)
131 FORMAT(Z)
MAXHOR=II*(ITIME-1)
WRITE(5,130)MAXHOR,0
WRITE(5,130)MAXHOR,1500
WRITE(5,131)0,1500
WRITE(5,130)0,0
```

```
132 WRITE(5,131)0,IB(1)
DO 133 I=2,ITIME
WRITE(5,130)II,IB(I)
II=II+IJ
133 CONTINUE
WRITE(3,134)
134 FORMAT(18HCHANGE PLOTTER PEN)
READ(3)OBS
WRITE(5,131)0,0
KOK=KOK+1
IF(KOK)136,136,137
136 DO 140 I=1,ITIME
140 IB(I)=IP(I)
II=IJ
GO TO 132
137 STOP
END
```